VOL. 86. Part 13. Pp. 239–246. 28th September, 1937.

MR. INST. ENT.
LIBRARY
28 SEP 1937
En. 344

THE

TRANSACTIONS

OF THE

ROYAL ENTOMOLOGICAL SOCIETY

OF

LONDON

Dimorphism in the males of Stag-Beetles (Coleoptera, LUCANIDAE).
By GILBERT J. ARROW . . . . . pp. 239–246, pls. 1–3

LONDON:
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

[*Price 5s. 0d.*]

THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

Founded, 1833. Incorporated by Royal Charter, 1885.

PATRON—HIS MAJESTY THE KING.

OFFICERS and COUNCIL for the SESSION 1937–1938.

A. D. Imms, M.A., Sc.D., F.R.S., *President.*

H. M. Edelsten
J. C. F. Fryer, O.B.E., M.A.
A. W. McKenny-Hughes, D.I.C. } *Vice-Presidents.*

Francis Hemming, C.B.E., *Treasurer.*

O. W. Richards, M.A., D.Sc., *Secretary.*

F. J. Griffin, A.L.A., *Registrar.*

Council.

R. B. Benson, M.A.
Prof. P. A. Buxton, M.A.
Brig.-Gen. B. H. Cooke, C.M.G., C.B.E., D.S.O.
H. Willoughby Ellis.
H. Eltringham, M.A., D.Sc., F.R.S.
G. Fox-Wilson.
Mrs. K. J. Grant.
L. G. Higgins, M.A., F.R.C.S.
B. M. Hobby, M.A., D.Phil.
J. A. Simes, O.B.E.
W. H. T. Tams.

Finance and House Committee.

Prof. P. A. Buxton, M.A. (Chairman).

C. L. Collenette.
H. Willoughby Ellis.
G. Fox-Wilson.
C. N. Hawkins.
C. B. Williams, M.A., Sc.D.

Publication Committee.

W. H. T. Tams (Chairman).

H. E. Andrewes.
M. Burr, D.Sc., F.G.S., A.R.S.M.
H. Eltringham, M.A., D.Sc., F.R.S.
B. M. Hobby, M.A., D.Phil.
V. B. Wigglesworth, M.A., B.Ch., M.D.

Library Committee.

J. C. F. Fryer, O.B.E., M.A. (Chairman).

R. B. Benson, M.A.
K. G. Blair, D.Sc.
E. A. Cockayne, M.A., M.D., F.R.C.P.
B. M. Hobby, M.A., D.Phil.
H. Scott, M.A., Sc.D.

Committee for the Protection of British Insects.

Rt. Hon. Lord Rothschild, D.Sc., F.R.S. (Chairman).

Capt. E. Bagwell-Purefoy, F.Z.S.
C. L. Collenette.
W. J. Dow.
J. C. F. Fryer, O.B.E., M.A.
Col. F. A. Labouchere.
N. D. Riley, F.Z.S.
W. G. Sheldon, F.Z.S.
H. M. Edelsten (Secretary).

The Executive Officers of the Society are *ex-officio* members of all Committees.

TRANSACTIONS AND PROCEEDINGS OF THE SOCIETY.

Some of the early volumes of the Society's Transactions are out of print. Any single volume of the years 1868–1887, is sold at 10*s.* to Fellows. The volumes for 1868–1900, in sets of not less than five, as well as the five of the Third Series (1862–1867), may be obtained by Fellows at greatly reduced prices on application to the Secretary. The following is a price list of recently published parts—

1934.—Transactions, Vol. LXXXII: Part I, £1 10*s.* 0*d.*, to Fellows, £1 2*s.* 6*d.*; Part II, £2 8*s.* 0*d.*, to Fellows, £1 16*s.* 0*d.*

Proceedings, Vol. IX: Part I, 4*s.* 0*d.*, to Fellows, 3*s.* 0*d.*; Part II, 6*s.* 0*d.*, to Fellows, 4*s.* 6*d.*; Part III, 12*s.* 0*d.*, to Fellows, 9*s.* 0*d.*

1935.—Transactions, Vol. LXXXIII: Part I, £2 12*s.* 0*d.*, to Fellows, £1 19*s.* 0*d.*; Part II, £1 10*s.* 0*d.*, to Fellows, £1 2*s.* 6*d.*; Part III, £1 13*s.* 0*d.*, to Fellows, £1 4*s.* 9*d.*; Part IV, £1 10*s.* 0*d.*, to Fellows, £1 2*s.* 6*d.*

Proceedings, Vol. X: Part I, 10*s.* 6*d.*, to Fellows, 7*s.* 9*d.*; Part II, 10*s.* 6*d.*, to Fellows, 7*s.* 9*d.*

STYLOPS.

1932–5.—Vols. 1–4, £1 16*s.* 0*d.* each; to Fellows, £1 7*s.* 0*d.*

Proceedings Series B. Taxonomy (being the continuation of *Stylops*).

1937.—Vol. 6 subscription £1 4*s.* 0*d.*

DIMORPHISM IN THE MALES OF STAG-BEETLES (COLEOPTERA, LUCANIDAE)

By Gilbert J. Arrow.

(*British Museum* (*Natural History*).)

[Read 5th May, 1937.]

With Plates 1 to 3.

In 1928, *Trans. ent. Soc. Lond.*, **76**, I published a paper on Polymorphism in Horned beetles, containing an account of various Dynastine and Coprine Coleoptera in which males of the same species exhibit markedly different phases in the horns borne on head and thorax. These different phases are in most cases linked together by individuals showing transitional stages, but in some cases no intermediates have been found, although large numbers of specimens have been examined.

A typical case of the latter kind is a large and abundant South American Dynastine beetle, *Enema pan* F. The male of this insect has a forked horn upon the thorax and a simple horn upon the head. I gave reasons for believing that another male form known as *E. infundibulum*, in which the conditions are reversed, the thoracic horn being simple and that of the head forked, is a phase of the same species, although no intermediate stages are found. The first-mentioned phase occurs in various degrees of development, the second is found in large specimens only and is almost constant.

At the time of writing my former paper I had made no study of the Stag-beetles (Lucanidae), but, having since devoted some time to studying the group, I have found that the mandibles of the male in many species exhibit the same curious phenomenon as I described in the horns of the other groups.

Although males and females of Dynastinae and Coprinae are frequently very dissimilar, there is no other group known to me in which such extreme dissimilarity occurs as in the Lucanidae, insects with larviform females only excepted. In the common Stag-beetle of southern England, *Lucanus cervus*, there is scarcely any external feature common to the two sexes. Shape, colour, surface-sculpture, form of the legs, antennae, jaws and other organs of the mouth, all are different. But in many other species the differences are much more striking. The male may in addition be uniformly coloured, while the female has conspicuous stripes, as in *Dorcus wimberleyi* and *Homoderus mellyi*, or, as in *Calcodes gazella*, male and female may have different patterns. In others the male is dull sooty black or brown, and the female glossy, as in *Dorcus saiga*, and in others again the male is smooth and the female deeply grooved along the back, as in *Dorcus curvipes* and *reichei*.

The correct association of the two sexes in this family is therefore a matter of exceptional difficulty. Unless many specimens are found in the same locality, evidence of specific identity may be entirely absent, and there are species which have been known for very many years of which the two sexes remain still unassociated.

Females as a rule show little variation except in size, but males are extremely variable, and two males of the same species may differ from one another as greatly as two specimens of opposite sex.

In discussing Polymorphism in Horned beetles, I drew attention to the fact that, in species with hornless females, the horns tend to disappear in dwarfed males, but that this is not the case when the female also is horned. In the same way, dwarfed male LUCANIDAE assume to a greater or less extent the characteristics of the female and may differ extremely from well-developed males. In *Dorcus saiga*, in which the female is glossy black, well-developed males are dull and sooty, but small examples are glossy like the female. Similarly, in *Dorcus tityus*, in which the female has deeply grooved elytra, dwarfed males are similarly grooved, but a series of specimens of gradually increasing size shows the gradual smoothing of the elytra until all trace of the grooves disappears. Until such series were brought together, isolated specimens were of necessity regarded as representing different species.

Although the changes which accompany increase of size affect almost every part of the body, they are generally most apparent in the mandibles. In many species the course of development of these is as follows. In the smallest males they are close together, with the inner edges in contact, straight, and finely and closely but irregularly toothed, a form evidently suited for gripping and probably primitive. This form is almost always lost in well-developed specimens. With increasing size the head becomes broader, the mandibles separated at the base, attenuated, bent or curved, at last meeting only at the tips, the teeth become fewer and larger, and fantastic shapes may be produced which by no means suggest fitness for any practical use.

Various recent authors have called attention to the correspondence between the degree of development of the mandibles and the size of the insect, and have shown that the former is mathematically determined by the latter. The rule, however, is subject to remarkable exceptions. In his Monograph * of the group of Stag-beetles which he called the Odontolabini Leuthner used various names, Priodont, Mesodont, Amphiodont and Telodont, to describe the mandibles in different stages of development, the primitive, finely toothed stage being called Priodont and the ultimate, most highly developed, condition Telodont. The comparatively small number of specimens available to him was insufficient to show that, whilst in all the lower stages every transition existed, the last (Telodont) stage in many cases formed a quite distinct and isolated phase. It is unfortunate that Dudich, in discussing the variation of the mandibles of a Lucanid (1923, *Arch. Naturg.*, **89** (A) 2 : 69), has used the term Telodont for an intermediate stage and introduced another, Mesamphiodont, for the extreme form.

When fairly large numbers of male LUCANIDAE of the same species are available, it will be found, by arranging them according to size, that in certain species, e.g. *Dorcus suturalis* Oliv. (pl. 3, figs. 1–2), the progressive development of the mandibles shows a rather remarkable interruption. At a certain point increase of bodily size ceases but that of the mandibles does not. Specimens are found, very rare in some cases but frequent in others (figs. 1*a*, 2*c*), in which the mandibles have attained considerably greater development unaccompanied by any further increase of bodily size. Such specimens are practically constant in form and not linked by intermediates with the progressive series into which the others range themselves. Leuthner, in the monograph just referred to, has figured side by side, as in *Calcodes* (*Odontolabis*) *burmeisteri* and *aeratus*, male specimens of identical size with entirely different mandibles. M. Paulian also has recently mentioned (1936, *Proc. zool. Soc. Lond.*, **1936** :

* 1885, *Proc. zool. Soc. Lond.*, **1885** : 385.

756) two species of *Odontolabis* in which there are two separate forms of male. Neither author, however, has dealt further with this curious fact.

Calcodes carinatus L. (pl. 1, fig. 4) is an abundant representative of its genus in Ceylon. In small examples (fig. 4*a*) the short mandibles, when closed, are in close contact and their inner edges are finely and irregularly toothed. In larger specimens (fig. 1*b*) the teeth are larger and farther apart, and in very well grown specimens a broad basal lobe and a long pointed tooth at some distance from it become isolated from the rest, leaving a considerable gap before and after the long tooth (fig. 4*c*). A series of about fifty males which I have examined show a gradual progression to this stage, at which the maximum size is reached. But thirteen specimens, all of large, but not larger size, (fig. 4*d*), have much longer and more slender jaws, which are entirely smooth to beyond the middle. The basal lobe and the long tooth have disappeared, but another slightly forked tooth has made its appearance towards the end. These thirteen specimens are all alike, and no connecting link between them and the ordinary progressive series can be found.

An exactly similar condition exists in various other species of the same genus. A common Himalayan species, *Calcodes cuvera*, may be mentioned as an example. Small males have mandibles similar to those of *Calcodes carinatus* but, with increasing size, the close irregular teeth become fewer and larger, and in large examples, in which the length of the jaws is almost equal to that of the head, a single long tooth appears detached from the rest near the base, the remaining teeth being irregular and unsymmetrical. This condition marks the end of the progressive stage in more than fifty males which I have examined, but there are other specimens in which the mandibles are much longer than the head, slender, symmetrical and without the long tooth before the middle, instead of which there is a forked branch beyond the middle and a sharp angle at the base. This form also is practically constant and is not connected with the inconstant form by any intermediate specimens. The two phases occur together in the same localities. The two phases of another very abundant Indian Stag-beetle, *Calcodes siva*, are shown in plate 1, fig. 2.

A Bornean member of the same genus, *Calcodes brookeanus* (pl. 1, fig. 3), shows the phenomenon still more strikingly. Small specimens have very broad flat jaws of nearly semicircular shape, their inner edges serrated and meeting. Except in size, this form shows little change until very large specimens are examined. These may have the teeth absent at the base (fig. 3*a*), leaving a small gap there, or they may have entirely different mandibles which, instead of being broad, are very slender, meeting only at the tips, which are acute, and with a long sharp tooth projecting inwards near the middle of each (fig. 3*b*). Here again a long series of specimens shows no connecting links.

A still more remarkable case is *Calcodes aeratus*, a Malayan species (pl. 3, fig. 3). This again has two entirely different types of male, an inconstant phase with a long head and triangular mandibles, with toothed edges in close contact (figs. 3*a*, 3*b*), and a constant phase (fig. 3*c*), with a broad head and mandibles which together almost form a circle, very slender and studded with fine teeth at regular intervals. Specimens of the inconstant phase vary in size from 15 mm. long to about 30 mm., and their mandibles at their maximum are shorter than the head. In the constant phase the mandibles are always much longer than the head and there is practically no variation.

The same phenomenon is found in several other species of *Calcodes*, and perhaps in most of them, but the constant phase may be very rare. A single specimen from the Philippine Is. in the British Museum, described 90 years

ago as *Calcodes dux*, was declared by Leuthner in 1885 to be in his opinion a form of *Calcodes alces*, and this specimen is still, so far as I know, the only example of the constant phase of that species. It seems quite possible that in some species this phase may only appear at long intervals of time.

Other cases of this interesting phenomenon are found in the genus *Dorcus*. *D. biplagiatus* Westw. (pl. 1, fig. 1), is a well-known and widely-distributed Indian Lucanid which exists in many collections, sometimes in considerable numbers. The mandibles of the ordinary male (fig. 1*b*) are of unusually small size, quite simple and no longer than the head even in the largest specimens. A single specimen in the Calcutta Museum and another in the British Museum (fig. 1*a*), both of them brought from the Andaman Islands, have mandibles of entirely different form, long and slender, with a tooth near the base, another before the tip, and between them a forked lobe. These specimens differ in no other respect from the normal form.

Of *Dorcus parryi* (pl. 2, fig. 3) I have seen eighty male examples. All but three of these have flat triangular mandibles, in close contact in small specimens, but in larger ones becoming separated at the base while the anterior halves remain in contact (fig. 3*c*). Of the eighty specimens two belong to the constant phase (fig. 3*a*) and have quite different mandibles, slender, curved and far apart, meeting only at the tips, the inner edges bearing only a few scattered teeth instead of the close rank found in the inconstant phase. There is also an erect tooth on the upper surface of the mandible, of which no trace appears in the inconstant phase. The third specimen (fig. 3*b*), which is in M. Oberthur's collection, is highly interesting. Like the two just mentioned, it is of maximum size. The left mandible is that of the rare constant phase, but the right is precisely that of a similar-sized example of the common phase.

In a Bornean species, *Dorcus forceps* (pl. 2, fig. 2), a single specimen in the British Museum also combines the two phases on different sides of the head (fig. 2*b*), the left mandible here being that of the inconstant and the right that of the constant form.

In *Dorcus faber* (pl. 3, fig. 4), a West African species of which the British Museum contains sixteen male examples, the constant phase appears to be the predominant one, while the inconstant is relatively rare. Thirteen specimens (fig. 4*a*) of this species have slender curved jaws meeting only at the tips and in only three they are short and flat, with the inner edges in contact (fig. 4*b*). In this case the specimens of the predominant form vary to some extent in the size, although not in the form, of the mandibles. It seems likely that here the primitive form is being displaced by the later one, which is assuming the character of variability. This seems to me to suggest that those LUCANIDAE, such as the genus *Lucanus*, in which the primitive Priodont type is never found, the mandibles being always widely separated, whatever the degree of development, have passed through that stage, and the earlier form, still predominant in others, has been replaced by the once-rare constant phase.

Other species in which two distinct male phases exactly like those already described may be found are *Calcodes burmeisteri*, *C. delesserti*, *C. sinensis*, *C. lowei*, *C. sommeri*, *C. stevensi*, *Dorcus serricornis*, and *D. antilope*. There are certainly many more in which the two phases exist, and probably some in which they are known by different names.

A single specimen from Assam in the Oxford University Museum (pl. 1, fig. 1*a*) was described by Hope a century ago under the name *Lucanus spencei*, and I believe that no similar specimen has ever been found. This insect has slender curved mandibles with a single small tooth near the base of each. A species

inhabiting the same region, which was named *Prosopocoelus mordax* by Boileau (pl. 1, fig. 1*b*), agrees with *spencei* in size, shape, and all else except in having massive serrate mandibles of completely different aspect. Boileau subsequently suggested the possibility that these might be two forms of the same species. Analogy with the nearly related *D. parryi* (pl. 2, fig. 3) makes it fairly certain that this is so. Identity of size in specimens of two phases of the same species can be regarded as evidence that no transitional stages exist, although it is only when a considerable series has been brought together that the absence of connecting links is plainly revealed.

In my opinion another rare Indian form, *Calcodes saundersi*, in which the mandibles are curved and bear an erect tooth at the base, may similarly be regarded as the constant phase of the very abundant *Calcodes baladeva*, in company with which it has been found. *C. baladeva* has the mandibles in close contact and always without trace of the basal tooth.

It may be stated as a general rule that when two such distinct forms of male appear side by side in the LUCANIDAE one is constant and the other variable. Those of the variable phase show every gradation from the smallest to the largest size, the jaws in small specimens are in close contact and not completely symmetrical. Specimens of the constant phase are of full size, their jaws are symmetrical, long, slender, far apart and meet only at the tips. There is no transition from one phase to the other. With few exceptions the constant phase is less abundant than the other; it is sometimes extremely rare and perhaps sometimes occurs only at long intervals of time.

Another kind of dimorphism also occurs in male LUCANIDAE. In certain wide-ranging species local forms are found of which the distinctive features appear only in the male sex and only in large specimens of that sex.

Dorcus giraffa (pl. 3, fig. 5) is an abundant insect in China, the Malay Peninsula, Java and other countries. The mandibles of the male are very long and slender, with numerous teeth distributed at intervals along the inner edge. In the best developed specimens they are almost straight for two-thirds of their length, bent outwards rather abruptly at that point and strongly rounded from there to the tip. A very large tooth is placed at the bend and the tip is forked. This form (fig. 5*b*) is common in Assam, but is not found in the Darjeeling district, where it is replaced by a form named *Dorcus arrowi* by Gravely (fig. 5*a*). The large males of this have the mandibles gently and uniformly curved, not forked at the end and without the strong tooth beyond the middle. The first tooth, occurring before the middle and always minute in the Assam form, is the largest in the Darjeeling form. This form has an East and West range from central China and Tonkin to the United Provinces of India. Gravely has stated that the females of the two forms are quite different, but the features which he enumerates as distinguishing the female of *D. arrowi* are all features peculiar to the male sex, and it is evident that he mistook the sex of the specimen described. Actually females from all localities are indistinguishable. All the distinctive features of the two forms are well marked in large males only, feeble in middle-sized individuals and entirely absent in very small specimens.

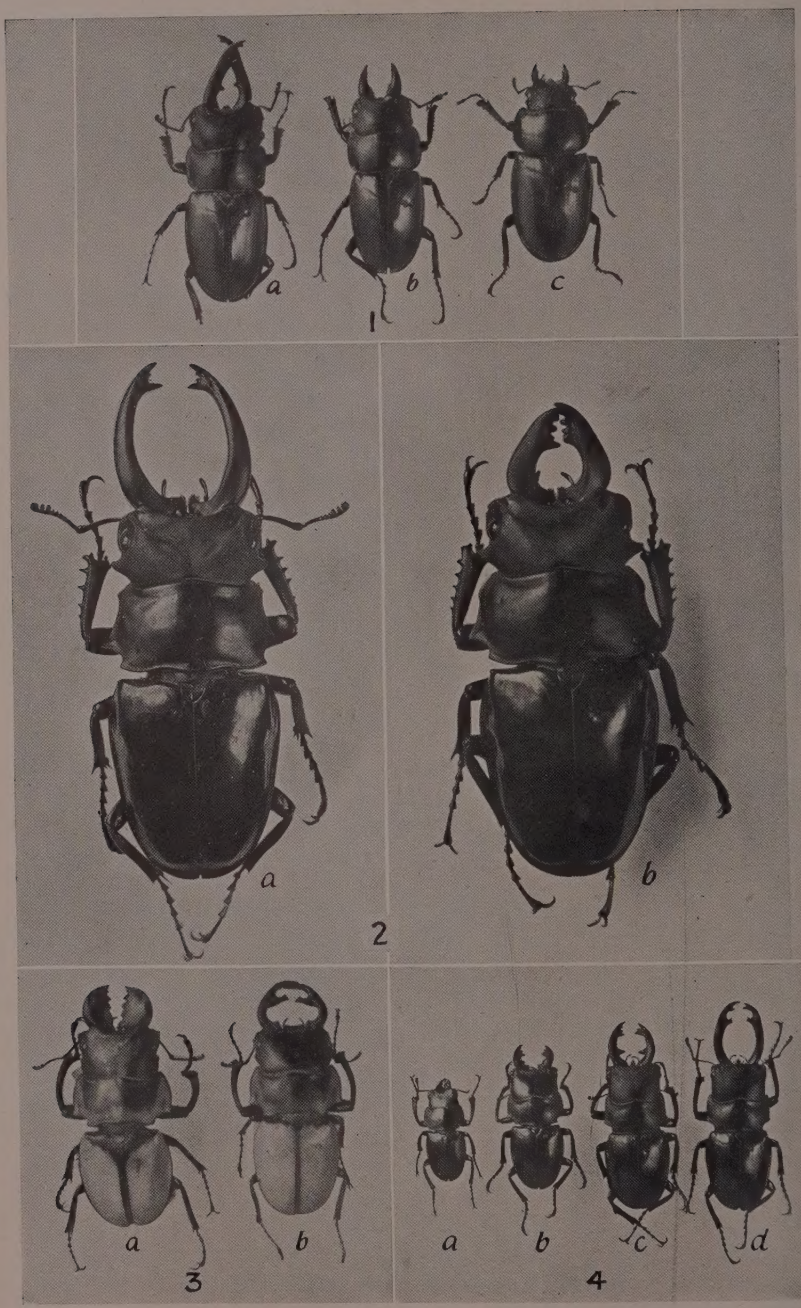
An exactly similar case of local variation in the male only is presented by another Indian species, *Dorcus foveatus* (pl. 3, fig. 6). A supposed distinct species inhabiting the Darjeeling district was described as *poultoni*. Full-sized males of this (fig. 6*a*) have teeth at intervals along the inner edge of the mandible, one before the middle and another beyond the middle being larger than the rest. Corresponding males from Assam (fig. 6*b*) have only one large

tooth which occupies a position between those of the two found in the Darjeeling form. The Assam form ranges as far as Upper Burma, but in Lower Burma a form called *birmanicus* is found. This also has only a single large mandibular tooth, which is placed near the base instead of near the middle of the mandible. These local differences exist only in large males. Small ones in all districts have the mandibles finely and closely toothed throughout. Females also are alike everywhere.

Another very common Stag-beetle, *Dorcus titanus*, is found in the East Indian Islands, the Malay Peninsula and India. The name *platymelus* has been given to a form found in China and Japan, which differs in the more slender mandibles of the male. But again this serves to distinguish only males of large size. Less well developed males cannot be separated, and females from all regions are alike.

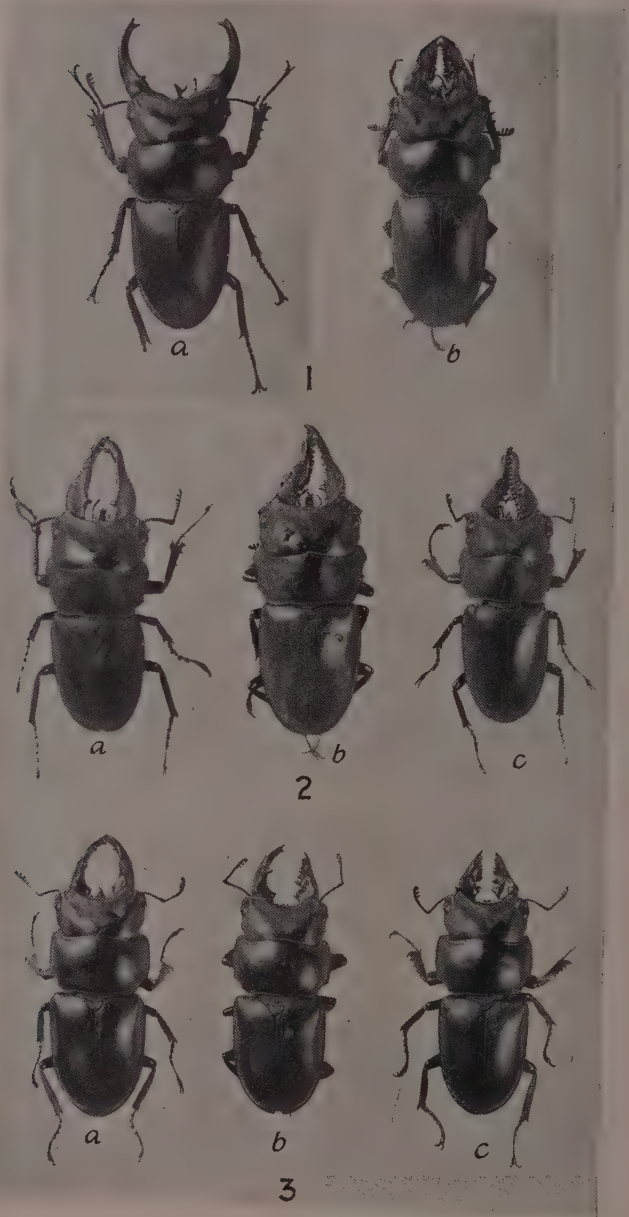
In beetles of the Lamellicorn families the highly chitinized aedeagus of the male often bears teeth and processes, sometimes of rather fantastic development and suggestively like the external horns and mandibular teeth so characteristic of the group. The question naturally arises whether the polymorphism which was long unsuspected in the external male characters can in any degree affect these internal structures also. Some recent authors rely upon their constancy to the extent of basing species upon them, even though no specific difference of any kind can be found in the other sex. There are no doubt groups in which these organs, as well as chitinous external structures, show a great degree of constancy; but, in the Lamellicornia at least they show considerable variability. In 1917, *Fauna of India* (Lamellicornia, 2: pl. 5, figs. 4–10) I have given a series of figures showing striking local variations in the aedeagus in a single wide-ranging species. Curti has also figured (1913, *Ent. Mitt.*, 2 : pl. 4, 5) a long series showing the local variation of the same organ in the common Rose-beetle, *Cetonia aurata*. Within a limited area the aedeagus appears to show considerable constancy, but, when studied in specimens from places more and more distant from the centre of an insect's range, more and more divergence of form may appear. This is the case in the Lucanid species just referred to, *Dorcus titanus*. Two pairs of converging spines upon the tegmen are separated by a distance which is found to vary slightly when examples from regions not far apart are examined; but comparison of specimens from countries as far removed as Japan and Assam shows a difference which appears very considerable.

In considering the question of specific differentiation, it appears to me that the relatively constant female of these insects is a better guide than the highly polymorphic male. Those who regard the female as of little importance will no doubt prefer to the conception of a single species with varying male forms that of many species with a single female form. Until there is agreement upon the precise meaning of the term species, both conceptions may be permissible; but while the former enables us to provide every specimen with a specific name, which is the object of the binomial system of nomenclature, the latter has the very obvious practical disadvantage that in many cases it completely fails when applied to one of the two sexes.



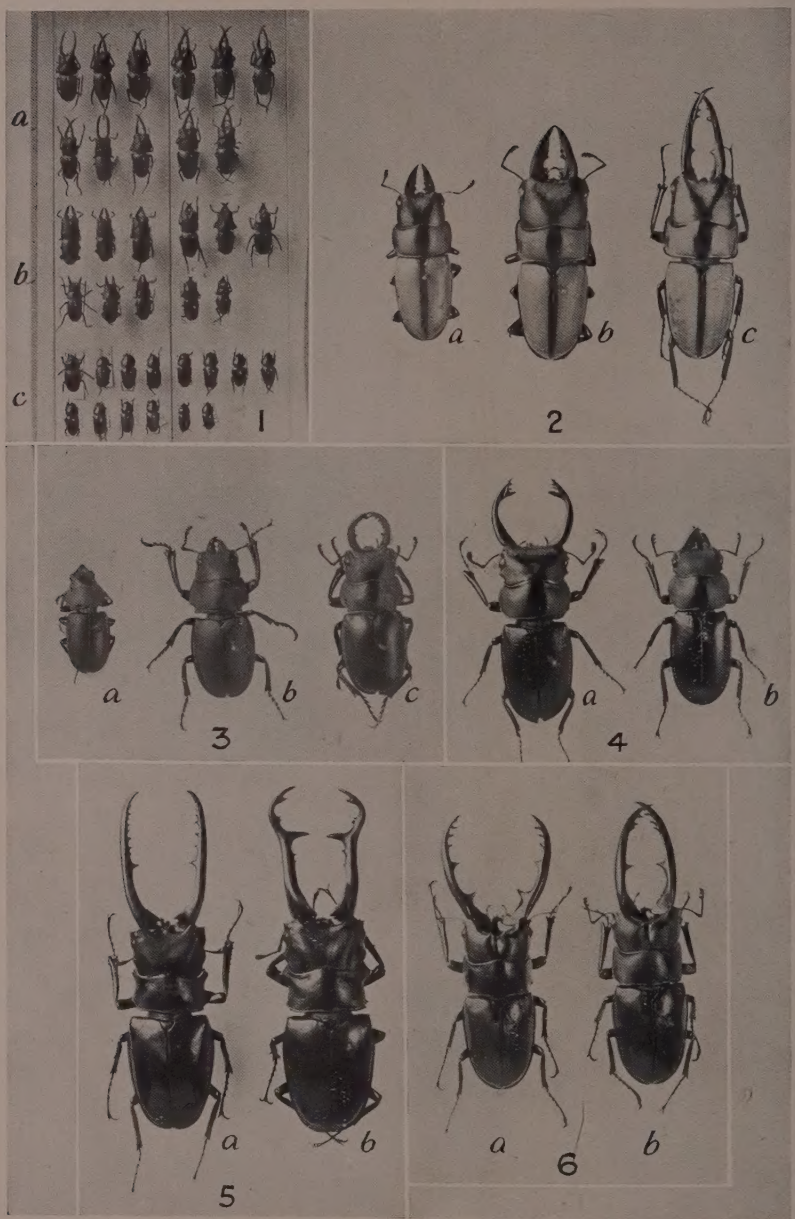
ENGRAVED BY STAR ILLUSTRATION, LONDON.

Dimorphism in male Lucanids.



ENGRAVED BY STAR ILLUSTRATION, LONDON.

Dimorphism in male Lucanids.



ENGRAVED BY STAR ILLUSTRATION, LONDON.

Dimorphism in male Lucanids.

Explanation of Plates.

Plate 1.

Fig. 1. *Dorcus biplagiatus* Westw., natural size. *a*. male, constant phase; *b*, male, variable phase; *c*. female.
2. *Calcodes siva* Hope, natural size. *a*. male, constant phase; *b*. male, variable phase.
3. *Calcodes brookeanus* Voll., natural size. *a*. male, variable phase; *b*. male, constant phase.
4. *Calcodes carinatus* L., reduced. *a*, *b*, *c*. males, variable phase; *d*. male, constant phase.

Plate 2.

Fig. 1. *Dorcus spencei* Hope, natural size. *a*. male, constant phase; *b*. male, variable phase.
2. *Dorcus forceps* Voll., natural size. *a*. male, constant phase; *b*. male, with both forms of mandible; *c*. male, variable phase.
3. *Dorcus parryi* Boil., natural size. *a*. male, constant phase; *b*. male, with both forms of mandible; *c*. male, variable phase.

Plate 3.

Fig. 1. *Dorcus suturalis* Oliv., reduced. *a*. males, constant phase; *b*. males, variable phase; *c*. females.
2. *Dorcus suturalis* Oliv., natural size. *a*, *b*. males, variable phase; *c*. male, constant phase.
3. *Calcodes aeratus* Hope, natural size. *a*, *b*. males, variable phase; *c*. male, constant phase.
4. *Dorcus faber* Thoms., natural size. *a*. male, constant phase; *b*. male, variable phase.
5. *Dorcus giraffa* F., reduced. *a*. male, *arrowi* phase; *b*. male, typical phase.
6. *Dorcus foveatus* Hope, reduced. *a*. male, *poultoni* phase; *b*. male, typical phase.